

Paternity data and relative testes size as measures of level of sperm competition in the Cercopithecoidea

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Historically, the empirical study of the role of sperm competition in the evolution of sexual traits has been problematic through an enforced reliance on indirect proxy measures. Recently, however, a procedure was developed that uses paternity data to measure sperm competition level directly in terms of males/conception (i.e., the number of males that have sperm present in a female's ampulla at conception). When tested on apes and humans (Hominoidea) this measure proved not only to correlate significantly with the traditionally used measure of relative testes size but also to offer a number of advantages. Here we provide a second test of the procedure, this time using paternity data for the Old World monkeys (Cercopithecoidea). We calculate sperm competition levels (males/conception) for 17 species of wild and free-ranging cercopithecoids and then analyze the data against measures of relative testes size. Calculated sperm competition levels correlate strongly with relative testes size both with and without phylogenetic control at both the species and generic levels. The signal-to-noise ratios inherent in both the past measure of relative testes size and the new measure of sperm competition level from paternity data are discussed. We conclude that although both measures are appropriate for the future study of the role of sperm competition in the evolution of sexual traits, when paternity data are available they provide the more direct and meaningful analytical tool. Not least, they potentially allow a first empirical analysis of the role of sperm competition in the evolution of relative testes size that could then be compared with the wealth of theoretical analyses that already exist.

KEYWORDS

multiple mating, Old World monkeys, paternity data, sexual trait evolution, signal/noise ratio

1 | INTRODUCTION

Sperm competition is the competition between sperm from multiple males to fertilize the egg(s) produced by a single female (Parker, 1970). In internal fertilizers, such competition occurs only when a female

“multiple-mates” (i.e., copulates with a further male or males while containing competitive sperm from an earlier but different male). To be directly involved in the production of offspring, this multiple-mating must occur when a fertilizable egg (or eggs) is already available in the female or will become available at some moment during the overlap in competitive lifetimes of the sets of sperm.

Since Parker's (1970) groundbreaking unveiling of the process of sperm competition for insects, students of sexual traits have recognized

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the widespread importance of the phenomenon as an evolutionary force (e.g., Smith, 1984). No matter whether the trait of interest is anatomical, physiological, behavioral, cellular, or molecular, nor whether the animal is an insect, fish, bird, mammal, or other, sperm competition is an ever-present candidate for influence. However, the empirical study of this influence has been, and still is, beset with difficulties. Prime among the problems has been the lack of means to measure sperm competition directly, forcing investigators to rely instead on indirect proxy measures as appropriate to different taxonomic groups.

For primates, two main proxy measures have been used: socio-sexual system (e.g., Harcourt, Harvey, Larson, & Short, 1981; Short 1979) and relative testes size (i.e., combined testes weight as a proportion of male body weight; e.g., of use see Anderson & Dixson, 2002; Dorus, Evans, Wyckoff, Choi, & Lahn, 2004). The adoption of socio-sexual system as a measure springs simply from the assumption that species with females living in groups containing multiple males will experience higher levels of sperm competition than those living in groups containing only a single male (Short, 1979). In contrast, the adoption of relative testes size as a measure derives from nearly five decades of theoretical modeling.

One group of such models (review: Parker, 2016) is based on the principle that the optimum number of sperm inseminated during copulation is an evolutionary trade-off between the risk that sperm may enter into competition with sperm from another male, favoring more sperm, and the cost of sperm production, favoring fewer. In consequence, if the level of sperm competition increases during the evolution of a lineage, then natural selection should favor males that inseminate more sperm until the advantage gained via sperm competition reaches the trade-off level.

In primates, more sperm can be produced at a faster rate by larger testes (Møller, 1988). Selection to increase the number of sperm inseminated should therefore result in males investing a greater proportion of resources into testes size (Parker 1970, 1982), thus leading to greater relative testes size (i.e., absolute testes size divided by total body weight, where absolute testes size is the weight of the two testes combined). Conversely, in lineages in which the trade-off level between sperm number and production cost begins to decrease because of decreasing levels of sperm competition, male investment in testes size should decrease and relative testes size will decrease accordingly. The predicted result is that, across species, those that evolved under higher levels of sperm competition should have a greater relative testes size than others that evolved under lower levels of sperm competition. Relative testes size, therefore, should be a correlate of the level of sperm competition during a species' evolutionary history and as a consequence can be used as a proxy measure of that level.

Empirically, the primary support for the validity of both measures (socio-sexual system and relative testes size) derives from a correlation between the two (Harcourt et al., 1981; Harcourt, Purvis, & Liles, 1995; Short, 1979).

Recently, we argued (Baker & Shackelford, 2018) that a third source of information, paternity data, may generate more than just a proxy measure of sperm competition level. We developed a procedure and formulae that allowed the direct calculation of sperm competition

level in terms of males per conception (i.e., the number of males that have sperm present in a female's ampulla at conception). So far, however, the support for the procedure and formulae developed in that article rests solely on an analysis of data for a single primate superfamily, the apes and humans (Hominoidea). Here we apply our procedure and formulae to data for the other superfamily of catarrhine primates, the Old World monkeys (Cercopithecoidea).

The hypothesis to be tested for the Cercopithecoidea in this article is the same as that tested previously for the Hominoidea (Baker & Shackelford, 2018). It is that paternity data, as processed here, can provide a measure of sperm competition that is at least as useful as relative testes size. We also take the first steps toward evaluating the accuracy of the levels of sperm competition (males/conception) calculated from paternity data and discuss whether this is a more practical or exploitable value than relative testes size to be used in future studies of the evolution of sexual traits.

2 | METHODS

As all data for cercopithecoids used here are from published studies by other authors, the protocol and procedures did not require review and approval by the IACUC or other institutional ethics committees overseeing animal use in research in either the United States of America or the United Kingdom. The study also adhered to the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates.

2.1 | Species referenced

A full list of the common and scientific names of all 28 species referenced in this article is provided in Table 1.

2.2 | Relative testes size

The relative testes size of cercopithecoids has been expressed as either (1) the combined weight of the paired testes as a simple percentage of male body weight (Harcourt et al., 1981) or (2) a residual measured from the regression of combined testes weight on body weight after log transformation of the data on both axes (Anderson & Dixson, 2002; Harcourt et al., 1995).

Table 2 lists the combined testes weight (gm), male body weight (kg), relative testes size (%), and residual testes size for 21 species. For nine genera it also shows the mean generic value calculated from the species for which testes data are presented. When data are available for only one species in a genus, the generic mean equals the value for the single species. When there are multiple species, the value for the genus is obtained by weighting the species-data phylogenetically. For this, we use Version 3 of the 10kTrees Website (Arnold, Matthews, & Nunn, 2010) to generate the consensus phylogeny, in Nexus format, of the primate species for which we have relevant data. This phylogeny (with branch lengths) has been sampled from a Bayesian phylogenetic analysis of genetic data. For analyses, we use version 3.0.1 (November 2017) of BayesTraits (Pagel & Meade, 2017). Among the procedures available in BayesTraits is the

TABLE 1 Taxonomic list of all species of Cercopithecoidea referenced

Taxon	Common English name	Scientific name	Authority
Superfamily	Old World Monkeys	Cercopithecoidea	
Family		Cercopithecidae	
Subfamily		Colobinae	
	King colobus	<i>Colobus polykomos</i>	Zimmermann, 1780
	Mantled guereza	<i>Colobus guereza</i>	Rüppell, 1835
	Ursine colobus	<i>Colobus vellerosus</i>	I. Geoffroy, 1834
	Golden snub-nosed monkey	<i>Rhinopithecus roxellana</i>	Milne-Edwards, 1870
	Northern plains gray langur	<i>Semnopithecus entellus</i>	Dufresne, 1797
	White-headed langur	<i>Trachypithecus poliocephalus</i>	Pousargues, 1898
	Dusky leaf monkey	<i>Trachypithecus obscurus</i>	Reid, 1837
	Silvery lutung	<i>Trachypithecus cristatus</i>	Raffles, 1821
Subfamily		Cercopithecinae	
Tribe		Cercopithecini	
	Red-tailed monkey	<i>Cercopithecus ascanius</i>	Audebert, 1799
	Blue monkey	<i>Cercopithecus mitis</i>	Wolf, 1822
	Patas monkey	<i>Erythrocebus patas</i>	Schreber, 1775
Tribe		Papionini	
	Assam macaque	<i>Macaca assamensis</i>	McClelland, 1840
	Toque macaque	<i>Macaca sinica</i>	Linnaeus, 1771
	Stump-tailed macaque	<i>Macaca arctoides</i>	I. Geoffroy, 1831
	Bonnet macaque	<i>Macaca radiata</i>	É. Geoffroy, 1812
	Southern pig-tailed macaque	<i>Macaca nemestrina</i>	Linnaeus, 1766
	Japanese macaque	<i>Macaca fuscata</i>	Blyth, 1875
	Crab-eating macaque	<i>Macaca fascicularis</i>	Raffles, 1821
	Rhesus macaque	<i>Macaca mulatta</i>	Zimmermann, 1780
	Barbary macaque	<i>Macaca sylvanus</i>	Linnaeus, 1758
	Mandrill	<i>Mandrillus sphinx</i>	Linnaeus, 1758
	Drill	<i>Mandrillus leucophaeus</i>	F. Cuvier, 1807
	Gelada	<i>Theropithecus gelada</i>	Rüppell, 1835
	Olive baboon	<i>Papio anubis</i>	Lesson, 1827
	Hamadryas baboon	<i>Papio hamadryas</i>	Linnaeus, 1758
	Guinea baboon	<i>Papio papio</i>	Desmarest, 1820
	Yellow baboon	<i>Papio cynocephalus</i>	Linnaeus, 1766
	Chacma baboon	<i>Papio ursinus</i>	Kerr, 1792

Nomenclature from Groves (2005).

facility to estimate the value of a trait, in this case relative testes size, at particular nodes internal to the phylogeny such as the most recent common ancestor of a specified congeneric group of species (Pagel, Meade, & Barker, 2004). To calculate the nodal value we use the random walk model and Markov chain Monte Carlo (MCMC) method.

2.3 | Paternity

The collection of paternity data from wild populations of primates involves obtaining genetic material from a sample of individuals and their potential parents, and then assigning paternity. The full list of

studies and study-groups plus the paternity data that form the basis of this article is presented in Table 3. The list includes all studies known to us of wild populations, including those populations that are habituated and/or partially provisioned. The list also includes all studies of free-ranging populations in their ancestral habitat, including those populations that are habituated and/or partially provisioned as long as they are not hormonally or otherwise manipulated in ways that could influence their sexual behavior. We exclude all studies of populations that the authors describe as “captive.” We also exclude all studies of populations introduced outside of their ancestral geographical range.

TABLE 2 Relative testes size

	Weights		Relative testes size			
	Testes	Body	Species		Genus (weighted)	
	(gm)	(kg)	(%)	Residual	(%)	Residual
Cercopithecoidea						
Colobinae						
<i>Colobus polykomos</i>	10.70	10.25	0.104	-0.232	0.070	-0.501
<i>Colobus guereza</i>	2.98	10.40	0.029	-0.795		
<i>Semnopithecus entellus</i>	11.10	17.00	0.065	-0.490	0.065	-0.490
<i>Trachypithecus obscurus</i>	4.80	7.45	0.064	-0.408	0.083	-0.331
<i>Trachypithecus cristatus</i>	6.20	6.58	0.094	-0.230		
Cercopithecinae						
Cercopithecini						
<i>Cercopithecus ascanius</i>	3.00	5.36	0.056	-0.435	0.056	-0.435
<i>Erythrocebus patas</i>	7.20	10.00	0.072	-0.391	0.072	-0.391
Papionini						
<i>Macaca arctoides</i>	48.20	10.51	0.459	+0.408	0.503	+0.393
<i>Macaca radiata</i>	48.20	8.65	0.557	+0.513		
<i>Macaca nemestrina</i>	66.70	9.98	0.668	+0.577		
<i>Macaca fuscata</i>	84.40	14.20	0.594	+0.489		
<i>Macaca fascicularis</i>	36.20	6.30	0.575	+0.560		
<i>Macaca mulatta</i>	46.40	9.20	0.504	+0.463		
<i>Mandrillus sphinx</i>	68.00	35.00	0.194	-0.092	0.212	-0.045
<i>Mandrillus leucophaeus</i>	41.05	20.00	0.205	-0.009		
<i>Theropithecus gelada</i>	17.10	20.40	0.084	-0.400	0.084	-0.400
<i>Papio anubis</i>	98.98	22.71	0.436	+0.304	0.256	+0.034
<i>Papio hamadryas</i>	58.62	20.78	0.282	+0.125		
<i>Papio papio</i>	88.90	31.98	0.278	+0.073		
<i>Papio cynocephalus</i>	52.00	24.32	0.214	-0.012		
<i>Papio ursinus</i>	72.00	31.75	0.227	-0.015		

Data shown only for genera for which paternity data are also available. Weights: Testes, combined weight of both testes (gm); Body, male body weight (kg). Data from Hamada et al. (2005), Harcourt et al. (1981, 1995), Jolly and Phillips-Conroy (2003), Luetjens and Weinbauer (2012). When mean values for a species occur in more than one publication the most recent is used. Relative testes size: %, testes weight as a percentage of male body weight; Residual, measured from the regression of combined testes size on body weight after log transformation of the data on both axes (+, testes heavier than expected; -, testes lighter than expected). Genus (weighted): Phylogenetically weighted means of all species in genus that are listed.

2.4 | Calculation of level of sperm competition from paternity data

The procedures and equations used here to calculate sperm competition level from paternity data were developed, described, and discussed by Baker and Shackelford (2018). Only a summary of the main features is provided here.

2.4.1 | Main data: Designated-Male and Other-Male paternity

The paternity of each female's offspring is expressed with respect to an individual male, here termed the Designated Male, chosen usually

by the original researchers from within that female's range of potential mating partners. Ideally, the Designated Male has a high (preferably ~100%) probability of having sperm present inside the female at the moment she conceives and is usually chosen by the researchers because he is in a recognizable behavioral or social category such as a consort or group alpha. If the female conceives to her Designated Male, the offspring is scored as a case of Designated-Male Paternity. All other males within a female's range of potential mating partners are here termed Other Males. Note that the Designated Male for one female can sometimes be an Other Male for another female. In this article we express the paternity data for a study-group as the percentage of young with Other-Male Paternity (OMP %).

TABLE 3 Paternity data

	Ref	Location	W/FR	D♂	DMP	OMP	OMP%
Cercopithecoidea							
<i>Colobus vellerosus</i>	1	Ghana	W/FR	a	6	1	14.3
	2		W/FR	a	4	4	50.0
	2		W/FR	S	1	3	75.0
<i>Rhinopithecus roxellana</i>	3	China (Qinling)	W	S	9	12	57.1
	4	China (Shennongjia)	FR	S	8	0	0.0
<i>Semnopithecus entellus</i>	5	S. Nepal	W	S	13	0	0.0
	5		W	a	17 †	13 †	43.1
<i>Trachypithecus poliocephalus</i>	6	China	W	S	20	1	4.8
<i>Cercopithecus mitis</i>	7	Kenya	W	R	67	54	44.6
<i>Erythrocebus patas</i>	8	Cameroon	W	S	2	2	50.0
	8		W	R	4	1	20.0
<i>Macaca assamensis</i>	9	Thailand	W	C	7 †	4 †	36.0
	9		W	a	11	27	71.1
<i>Macaca sinica</i>	10	Sri Lanka	W	S	7	0	0.0
	10		W	PF	6	12	66.7
<i>Macaca fuscata</i>	11	Yakushima Island	W	a	2	7	77.8
	12		W	(a+β)/2	1	7	87.5
<i>Macaca fascicularis</i>	13	N. Sumatra	W	S	12	1	7.7
	13		W	a	8	3	27.3
	13		W	a	12	9	42.9
	14		W	HA	2	4	66.7
<i>Macaca mulatta</i>	15	China (Jiyuan)	W/FR	a	1	7	87.5
<i>Macaca sylvanus</i>	16	Gibraltar	W	a	1	17	94.4
	17		W	Thorán	4	8	66.7
<i>Mandrillus sphinx</i>	18	Gabon	FR	a	147	46	23.8
<i>Theropithecus gelada</i>	19	Ethiopia	W	S	47	0	0.0
	19		W	a	24	5	17.2
<i>Papio cynocephalus</i>	20	E. Africa	W	Radi	22	5	18.5
	21		W	a	49	96	66.2
<i>Papio hamadryas</i>	22	Saudi Arabia	W	S	1	6	85.7
	22		W	S	1	5	83.3
	22		W	S	1	2	66.7
<i>Papio ursinus</i>	23	Namib Desert	W	a	5	7	58.3
	23		W	a	8	1	11.1

References: 1, Teichroeb, Wikberg, Ting, and Sicotte (2013); 2, Fox (2015); 3, Guo, Ji, Li, Chang, and Li (2010); 4, Xiang et al. (2014); 5, Launhardt, Borries, Hardt, Epplen, and Winkler (2001); 6, Liu et al. (2013); 7, Roberts, Nikitopoulos, and Cords (2014); 8, Ohsawa, Inoue, and Takenaka (1993); 9, Sukmak, Wajjwalku, Ostner, and Schülke (2014); 10, Keane, Dittus, and Melnick (1997); 11, Soltis et al. (2001); 12, Hayakawa (2008); 13, De Ruiter, Van Hooff, and Scheffrahn (1994); 14, Engelhardt et al. (2006); 15, Wang, Wang, Tian, Cui, and Lu (2015); 16, Kümmerli and Martin (2005); 17, Brauch et al. (2008); 18, Charpentier et al. (2005); 19, Snyder-Mackler, Alberts, and Bergman (2012); 20, Altmann et al. (1996); 21, Alberts, Buchan, and Altmann (2006); 22, Yamane, Shotake, Mori, Boug, and Iwamoto (2003); 23, Huchard et al. (2010, 2013). W/FR: W, Wild; FR, free-ranging; W/FR, in natural habitat with some degree of restriction of movement due to isolated or fragmented habitats. D♂, Designated Male: a, alpha male of multi-male, multi-female group; S, sole male in a uni-male, multi-female group; R, resident male in a group that is sometimes uni-male and sometimes multi-male; β, beta male; C, consort; PF, previous father (i.e., sire of a female's previous infant); HA, Thorán, Radi, named individuals. DMP, Designated-Male Paternities; OMP, Other-Male Paternities; OMP%, percentage Other-Male Paternities. †, rounded integers for studies in which the original authors, through uncertainty, either divided some paternities among males or gave a rounded value for OMP% that did not convert precisely into integers.

2.4.2 | Sampling bias and correction

None of the values of OMP % for individual studies or study-groups presented in Table 3 can be considered representative of whole species or even whole subpopulations for two reasons: (1) in most cases the primary data are based on small samples from local subpopulations and (2) none of the primary samples involved structured sampling designed to yield data representative of a wider population. We have discussed this issue previously (Baker & Shackelford, 2018) and there employed such corrective procedures as possible whenever these could lead to a reduction in sampling bias.

Here, when data are available, we use three factors to produce a weighted mean for OMP % before running the calculations described below. These are (1) sample size (i.e., total number of paternities assigned in a study-group); (2) relative long-term contribution of offspring to the next generation by each group studied (quantified as the number, or mean number, of adult females in each group); and (3) relative frequency of each type of group in the population (e.g., uni-male vs. multi-male groups, or “small groups” vs. “large groups”). The full list of weighting factors and resulting weighted means is given in Table 4.

2.4.3 | Subsidiary data

Although Designated-Male Paternity and Other-Male Paternity are the primary data needed, the formulae used to calculate sperm competition level from paternity data also require values for two subsidiary variables (i.e., subsidiary in the sense that if no usable field data exist, default values can be allocated). The variables are (1) Percentage of Other-Male matings that are Multiple-matings (POM, default = 100) and (2) Fertilization Bias (FB, default = 1.0). In this article, for reasons given in the Discussion, POM is treated as a constant with a value of 100% (n.b. use of the term “Multiple-matings” in this article rather than the more traditional term “Double-matings” used in Baker and Shackelford (2018) has required the parameter POD used there to be changed to POM here).

Fertilization Bias is the ratio of observed to randomly expected “wins” by Designated Males during sperm competition. When sperm from the average Designated Male in the sample and the average Other Male in the sample have equal chances of “winning,” then FB = 1. When circumstances favor fertilization by sperm from the average Designated Male in the sample, then FB > 1. When FB < 1, it conveys that circumstances favor fertilization by sperm from the average Other Male to an extent given by 1/FB. The calculated values of Fertilization Bias for 17 species are listed in Table 5.

2.4.4 | Equations

The three equations used to calculate the level of sperm competition from paternity data in this article are as follows:

$$FSC = \{100\} * \{[OMP] * [POM/100] * [1 + (FB/(ISC - 1))]\} / \{DMP + OMP\} \quad (1)$$

$$ISC = \{[FB] / \{[(DMP + OMP) * FSC] / (OMP * POM)\} - 1\} + 1 \quad (2)$$

$$LSC = 1 + [(FSC/100) * (ISC - 1)] \quad (3)$$

where FSC is the frequency of sperm competition (i.e., the proportion of offspring, range 0–100%, whose conception follows a bout of sperm competition between two or more males); DMP is the number or percentage of Designated-Male Paternities; OMP is the number or percentage of Other-Male Paternities; POM is the percentage of Other-Male matings that are multiple-matings involving at least the Designated Male and perhaps others; ISC is the intensity of sperm competition (i.e., the number of males, range 2 to n , and including the Designated Male, that have sperm inside the female at conception when sperm competition occurs); FB is the fertilization bias; and LSC is the level of sperm competition (i.e., the mean number of males, range 1 to n , whose sperm are present at each conception, including occasions when no sperm competition occurs).

Expressed in relation to the now-standard mathematical terms used, for example, by Parker (2016), $FSC = q * 100$, $ISC = N$ (when $FSC = 100$), $LSC = 1 + q$ (when $FSC < 100$), and $LSC = N$ (when $FSC = 100$). Although Parker (2016) separates his models into two, the “risk” model (when, in our terms, $LSC < 2$) and the “intensity” model (when, in our terms, $LSC \geq 2$), our use of LSC in this article is as a continuous variable identical to the “Number of ejaculates in competition” shown as the x-axis in Parker (2016; Figure 2).

A full account of the development and rationale of these formulae along with a detailed exposition of caveats and other considerations is presented in Baker and Shackelford (2018).

2.4.5 | Procedure

The following procedure is that developed, discussed, and justified in Baker and Shackelford (2018). First, use Equation (1) to calculate the frequency of sperm competition (FSC) with intensity (ISC) set to its minimum value of two males. If the value of FSC calculates to be less than 100%, then the frequency of sperm competition is accepted as calculated, the intensity of sperm competition is accepted to be two males, and the level of sperm competition (LSC, henceforth usually referenced simply as “sperm competition level”) can be calculated from Equation (3). However, if, with $ISC = 2$, Equation (1) yields a value for FSC that is >100%, an additional step is necessary before calculating LSC. Set the value of FSC to 100 and then use Equation (2) to calculate ISC. These are then the values of FSC and ISC used to calculate sperm competition level from Equation (3).

Additional considerations and limitations to this procedure are discussed in Baker and Shackelford (2018) but do not affect any of the calculations in this article. A spreadsheet that automatically calculates frequency, intensity, and level of sperm competition from paternity data with all constraints applied is provided as supplementary information to Baker and Shackelford (2018).

TABLE 4 Other-male paternity: Calculation of weighted means

	Study	Weighting factor value			Weighted mean	
	OMP (%)	Sample size	♀♀	Proportion	Type	OMP (%)
<i>Colobus vellerosus</i>	14.3	7	8.8	0.63/2	♂♂	34.8
	50.0	8	5.0	0.63/2	♂♂	
	75.0	4	3.5	0.37	♂	
<i>Rhinopithecus roxellana</i>	57.1	21	5.6	-		43.8
	0.0	8	4.5	-		
<i>Semnopithecus entellus</i>	0.0	13	4.8	0.28	♂	38.6
	43.1	29	7.2	0.72	♂♂	
<i>Trachypithecus poliocephalus</i>	4.8	-	-	-		4.8
<i>Cercopithecus mitis</i>	44.6	-	-	-		44.6
<i>Erythrocebus patas</i>	50.0	4	-	0.50	♂	33.3
	20.0	5	-	0.50	♂♂	
<i>Macaca assamensis</i>	36.0	11	-	0.79	C	53.0
	71.1	38	-	0.21	OM	
<i>Macaca sinica</i>	0.0	7	3.5	0.38	♂	61.5
	66.7	18	10.0	0.62	♂♂	
<i>Macaca fuscata</i>	77.8	9	15.0	-		79.6
	87.5	8	4.0	-		
<i>Macaca fascicularis</i>	7.7	13	3.0	0.05	Sg1	51.7
	27.3	11	4.5	0.08	Sg2	
	42.9	21	12.0	0.15	Lg	
	66.7	6	8.0	0.72	Mog	
<i>Macaca mulatta</i>	87.5	-	-	-		87.5
<i>Macaca sylvanus</i>	94.4	18	9.0	-		79.6
	66.7	12	15.5	-		
<i>Mandrillus sphinx</i>	23.8	-	-	-		23.8
<i>Theropithecus gelada</i>	0.0	47	5.1	0.67	♂	4.7
	17.2	29	6.3	0.33	♂♂	
<i>Papio cynocephalus</i>	18.5	27	16.7	-		58.1
	66.2	145	15.2	-		
<i>Papio hamadryas</i>	85.7	7	5.0	-		82.1
	83.3	6	2.0	-		
	66.7	3	3.0	-		
<i>Papio ursinus</i>	58.3	12	16.0	-		44.3
	11.1	9	9.0	-		

Order of studies and reference sources as in Table 3, plus supplementary information for weighting factors from references in Table 5. Weighting factor values: Sample size, number of paternities assigned; ♀♀, mean number of females in the study-group; Proportion (type), either the proportion of the wider population that is of the studied type or (as appropriate) the proportion of young conceived that are from this source. ♂, uni-male group; ♂♂, multi-male group; C, consorts; OM, opportunistic mating; Sg1, small group with 1-2 males; Sg2, small multi-male (3-4) group; Lg, large multi-male (>8) group; Mog, modal-sized multi-male (5-7) group; -, indicates a value is either unavailable or unnecessary and so the factor is not used in weighting. Weighted mean: Mean value of OMP (%) for each species.

2.4.6 | Statistics

All standard parametric analyses without phylogenetic correction in this article were generated using the Real Statistics Resource Pack software (Release 5.4; Zaiantz, 2018). Correlation analyses with phylogenetic

correction were performed as described by Pagel and Meade (2017). For the primate species for which we have relevant data we use Version 3 of the 10kTrees Website (Arnold et al., 2010) to generate the consensus phylogeny, in Nexus format. We then use the Independent Contrasts facility in version 3.0.1 (November 2017) of BayesTraits (Pagel & Meade,

TABLE 5 Assessment of fertilization bias from observational and paternity data

	Field evidence		
	Overt	Cryptic	FB
<i>Colobus vellerosus</i>	0		1.0
<i>Rhinopithecus roxellana</i>	++	-	2.0
<i>Semnopithecus entellus</i>	0		1.0
<i>Trachypithecus poliocephalus</i>			1.0
<i>Cercopithecus mitis</i>	+		2.0
<i>Erythrocebus patas</i>	+	-	1.0
<i>Macaca assamensis</i>	+		2.0
<i>Macaca sinica</i>			1.0
<i>Macaca fuscata</i>	+		2.0
<i>Macaca fascicularis</i>	++	+	4.0
<i>Macaca mulatta</i>	+	- -	0.5
<i>Macaca sylvanus</i>	0	-	0.5
<i>Mandrillus sphinx</i>	++		3.0
<i>Theropithecus gelada</i>	++	-	2.0
<i>Papio cynocephalus</i>	++	0	3.0
<i>Papio hamadryas</i>	++	- -	1.0
<i>Papio ursinus</i>	++	0	3.0

Field evidence from references in Table 3 with additional data on behavior for: *Colobus vellerosus* (Teichroeb & Sicotte, 2010); *Semnopithecus entellus* (Heistermann et al., 2001); *Cercopithecus mitis* (Cords, Mitchell, Tsingalia, & Rowell, 1986; Roberts & Cords, 2015); *Erythrocebus patas* (Harding & Olson, 1986); *Macaca assamensis* (Fürstbauer, Heistermann, Schülke, & Ostner, 2011; Schülke, Bhagavatula, Vigilant, & Ostner, 2010); *Macaca sinica* (Dittus, 1988); *Macaca fascicularis* (Van Noordwijk & Van Schaik, 1985); *Mandrillus sphinx* (Dixon et al., 1993; Setchell et al., 2005); *Theropithecus gelada* (Le Roux, Snyder-Mackler, Roberts, Beehner, & Bergman, 2013); *Papio cynocephalus* (Altmann & Alberts, 2003); *Papio hamadryas* (Kummer, 1968; Nystrom, 1992; Swedell, 2006; Swedell & Saunders, 2006); *Papio ursinus* (Bulger, 1993; Hall 1962; Palombit, 2003). Overt (++, strong observed skew in mating frequency in favor of Designated Male; +, weak observed skew in favor of Designated Male; 0, no observed skew); Cryptic (+, skew in paternity even more strongly in favor of Designated Male than mating frequency; 0, paternity skew matches mating frequency skew; -, paternity skew less strongly in favor of Designated Male than mating frequency skew; - -, paternity skew much less strongly in favor of Designated Male than mating frequency skew). Empty cells indicate no relevant data. FB, fertilization bias. Each plus in the Overt and Cryptic columns is given a value of +1, each 0 and empty cell a value of 0, and each minus a value of -1. When the sum (S) of the cell values is positive, $FB = 1 + S$. When S is negative, $FB = -1/(-1 + S)$.

2017) for correlation analysis. The generated statistic (LogBF) is then interpreted as showing either “no positive evidence,” “positive evidence,” “strong evidence,” or “very strong evidence” following Raftery (1996).

3 | RESULTS

3.1 | Sperm competition level and relative testes size

Table 6 lists 28 species of cercopithecoidea for which measures of sperm competition level and/or relative testes size are used in this

article. Relative testes size is presented both as a simple percentage of body weight, and as a residual.

Phylogenetically weighted means for sperm competition level can be calculated for 10 genera (Table 6). However, for only six of these genera (if we restrict calculation to species for which a measure of relative testes size is also available), is it possible to calculate matching weighted means for relative testes size. If we relax this restriction to make maximum use of the available data we can then calculate phylogenetically weighted means for nine genera. These are the genera which contain at least one species with a measure for sperm competition level and at least one species with a measure for relative testes size, even though these species may not always be the same.

The generic means for the six genera in the column labeled residual-3 in Table 6 are residuals calculated by Anderson and Dixon (2002) from a regression of testes weight on male body weight for a wide range of primate groups, not just cercopithecoidea.

3.2 | Correlations between sperm competition level and relative testes size

Table 7 shows the degree of correlation (both with and without phylogenetic correction) between all equivalent measures of sperm competition level and relative testes size. All are either strongly or very strongly significant. We conclude for the Cercopithecoidea, as for the Hominoidea (Baker & Shackelford, 2018), that paternity data yield a measure of sperm competition level (as males/conception) that correlates strongly with relative testes size (however measured) at both the species and generic levels.

3.3 | Comparison with a theoretical curve from Parker (2016)

Parker (2016, Figure 2) presents a theoretical curve which shows the optimal variation in relative testes size at different sperm competition levels. In Figure 1, we show both a linear ($y = 0.07x + 0.005$; $R^2 = 0.681$; $F_{1,8} = 17.063$; $p = 0.003$) and a log plot of our cercopithecoidea data for 10 species from Table 6. Parker's theoretical curve is then superimposed on the log plot (Figure 1b). Parker's x-axis scale (number of ejaculates in competition) and our own (males/conception) are not only identical in terms of units but also span a nearly identical range (Parker: 1–10; Table 6: ~1 to ~9). They can therefore be matched exactly and objectively in Figure 1b. Unavoidably, however, Parker's y-axis (relative testes size) is dimensionless and so can be matched only subjectively. We opted to superimpose Parker's curve so that (a) the maximum values of the two curves are equal and (b) the minimum value on Parker's curve (where $x = 1.0$ males/conception, i.e., zero sperm competition) is positioned at a level below the smallest relative testes size plotted. Any statistical evaluation of a curve fitted to data in this subjective way would be meaningless, but visually the match between the two is at least cross-supportive, both for the data generated here and for Parker's theoretical curve itself.

TABLE 6 Data for comparison of sperm competition level and relative testes size

Species	Sperm competition level				Relative testes size		
	Males/conception				%	Residual	
<i>Colobus vellerosus</i>	1.697				-	-	
<i>Colobus polykomos</i>	-				0.104	-0.232	
<i>Colobus guereza</i>	-				0.029	-0.795	
<i>Rhinopithecus roxellana</i>	2.556				-	-	
<i>Semnopithecus entellus</i>	1.772				0.065	-0.490	
<i>Trachypithecus poliocephalus</i>	1.100				-	-	
<i>Trachypithecus obscurus</i>	-				0.064	-0.408	
<i>Trachypithecus cristatus</i>	-				0.094	-0.230	
<i>Cercopithecus mitis</i>	2.612				-	-	
<i>Cercopithecus ascanius</i>	-				0.056	-0.435	
<i>Erythrocebus patas</i>	1.667				0.072	-0.391	
<i>Macaca arctoides</i>	-				0.459	+0.408	
<i>Macaca assamensis</i>	3.256				-	-	
<i>Macaca radiata</i>	-				0.557	+0.513	
<i>Macaca sinica</i>	2.600				-	-	
<i>Macaca nemestrina</i>	-				0.688	+0.577	
<i>Macaca fuscata</i>	8.824				0.594	+0.489	
<i>Macaca fascicularis</i>	5.283				0.575	+0.560	
<i>Macaca mulatta</i>	4.500				0.504	+0.463	
<i>Macaca sylvanus</i>	2.951				-	-	
<i>Mandrillus sphinx</i>	1.953				0.194	-0.092	
<i>Mandrillus leucophaeus</i>	-				0.205	-0.009	
<i>Theropithecus gelada</i>	1.141				0.084	-0.400	
<i>Papio anubis</i>	-				0.436	+0.304	
<i>Papio hamadryas</i>	5.600				0.282	+0.125	
<i>Papio papio</i>	-				0.278	+0.073	
<i>Papio cynocephalus</i>	5.165				0.214	-0.012	
<i>Papio ursinus</i>	3.388				0.227	-0.015	
Genera	SCL-1	SCL-2	%-1	%-2	Residual-1	Residual-2	Residual-3
<i>Colobus</i>	-	1.697	-	0.070	-	-0.501	-
<i>Rhinopithecus</i>	-	2.556	-	-	-	-	-
<i>Semnopithecus</i>	1.772	1.772	0.065	0.065	-0.490	-0.490	-
<i>Trachypithecus</i>	-	1.095	-	0.083	-	-0.331	-
<i>Cercopithecus</i>	-	2.612	-	0.056	-	-0.435	-0.18
<i>Erythrocebus</i>	1.667	1.667	0.072	0.072	-0.391	-0.391	-1.25
<i>Macaca</i>	4.574	4.031	0.511	0.503	+0.400	+0.393	+0.84
<i>Mandrillus</i>	1.953	1.953	0.194	0.212	-0.092	-0.045	+0.37
<i>Theropithecus</i>	1.141	1.141	0.084	0.084	-0.400	-0.400	-0.75
<i>Papio</i>	4.257	4.257	0.259	0.256	+0.038	+0.034	+0.54

Sperm competition level: males/conception. Relative testes size: %, combined testes weight as percentage of male body weight; residual, measured from the regression of combined testes size on body weight after log transformation of the data on both axes (+, testes heavier than expected; -, testes lighter than expected). Species: Sperm Competition level (SCL) - calculated from the data in Tables 3-5 using the procedures and formulae in Baker and Shackelford (2018) with POM = 100; Relative Testes Size - from Table 2. Genera: Values for both Sperm Competition and Relative Testes Size are phylogenetically weighted means; -, missing values. SCL-1, %-1, residual-1: Generic means calculated using only species for which data are available for both sperm competition level and relative testes size; SCL-2, %-2, residual-2: Generic means calculated using all species for which data are available; residual-3: Generic means from Anderson and Dixon (2002).

TABLE 7 Correlations between sperm competition level and relative testes size

Correlation	Without phylogenetic correction			With phylogenetic correction		
	Pearson's <i>r</i>			Independent contrasts		
	<i>n</i>	<i>r</i>	<i>p</i> (1-tailed)	<i>n</i>	<i>logBF</i>	Strength (2-tailed)
Species						
SCL vs. RTS (%)	10	0.825	0.002	10	7.5	"Strong"
SCL vs. RTS (residual)	10	0.820	0.002	10	7.6	"Strong"
Genus						
SCL-1 vs. RTS (%)	6	0.884	0.010	6	9.7	"Strong"
SCL1 vs. RTS (residual-1)	6	0.896	0.008	6	10.6	"Very strong"
SCL-2 vs. RTS (%)	9	0.773	0.007	9	7.3	"Strong"
SCL-2 vs. RTS (residual-2)	9	0.771	0.008	9	7.8	"Strong"
SCL-2 vs. RTS (residual-3)	6	0.796	0.029	6	6.7	"Strong"

Correlation analysis, without and with phylogenetic correction, using data from Table 6. SCL, sperm competition level (males/conception) (SCL-1, SCL-2 as defined in Table 6); RTS, relative testes size (% residual, residual-1, residual-2; residual-3; see Table 6).

3.4 | Comparison of calculated and observed levels of sperm competition

Two major obstacles prevent the direct measurement of sperm competition level via simple field observation of primate mating behavior: (1) the impossibility of recording, day and night, all the males with which a given female mates and (2) the difficulty of knowing precisely when, in terms of observation days, each female is or was in her conceptive fertile phase. Other obstacles also exist but need not be considered here. Obstacle (1) has not yet been overcome, but a combination of the collection of hormonal and birth data has allowed some progress in circumventing obstacle (2).

Three studies of cercopithecoids have so far yielded relevant mating data by females on days that were likely to have been within conceptive fertile phases: (1) Dixon et al. (1993) observed females of *Mandrillus sphinx* mating with an average of 1.46 males/conception (range 0–3); (2) Fürtbauer et al. (2011) recorded female *Macaca assamensis* mating with a mean of 2.2

males/conception (range 1–4); and (3) Engelhardt, Heistermann, Hodges, Nürnberg, and Niemitz (2006) observed females of *Macaca fascicularis* mating with a mean of 2.7 males/conception (range 1–5) if they were "monopolized" by alpha males, but with a mean of 5.2 males/conception (range 4–7) if they were consorted by alpha and/or other males but not monopolized (unweighted mean = $(2.7 + 5.2)/2 = 3.95$ males/conception).

As none of these authors expected or claimed to have observed all the matings by the females concerned, these three figures of 1.46, 2.20, and 3.95 males/conception would each be expected to be an underestimate of the true sperm competition level. This expectation is consistent with the figures, respectively, of 1.95, 3.26, and 5.28 males/conception calculated from paternity data (Table 6).

If the figures from paternity data in Table 6 were accurate estimates of sperm competition level, the implication would be that the field observers did not see an average of 25%, 32%, and 25%, respectively, of the females' total mating partners. Or, expressed another way, over the 5–6 day course of a whole conceptive fertile

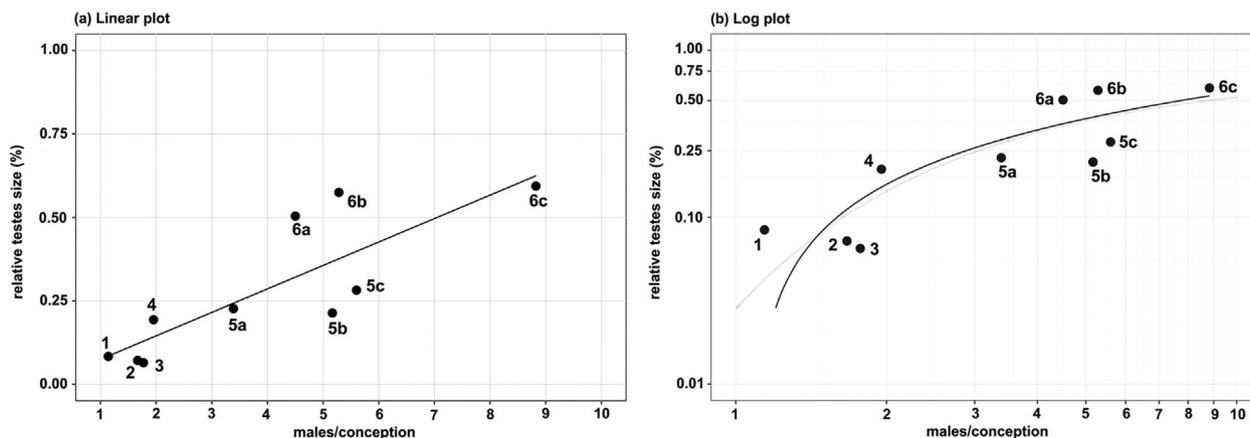


FIGURE 1 Linear and log plots of relative testes size on sperm competition level for 10 species of cercopithecoids. Data from Table 6. 1, *Theropithecus gelada*; 2, *Erythrocebus patas*; 3, *Semnopithecus entellus*; 4, *Mandrillus sphinx*; 5a, *Papio ursinus*; 5b, *Papio cynocephalus*; 5c, *Papio hamadryas*; 6a, *Macaca mulatta*; 6b, *Macaca fascicularis*; 6c, *Macaca fuscata*. In (b) the black curve is the logarithmic fit to the data and the gray curve is a superimposed theoretical curve taken from Parker (2016)

phase they missed a given female mating with an average of 0.49 (*Mandrillus sphinx*), 1.06 (*Macaca assamensis*), and 1.33 (*Macaca fascicularis*) additional males.

4 | DISCUSSION

All scientific measurements have sources of error. These errors create a signal-to-noise ratio in the data that is less than the optimal infinity (as generated by noise = 0) (Trout, 1998). From the available evidence discussed below, however, for neither relative testes size nor sperm competition level (as calculated here) is the signal-to-noise ratio so low that the measure has no analytical value.

4.1 | Signal-to-noise ratio: Relative testes size

To obtain a figure for relative testes size for a species, two measures are needed: testes weight and body weight. Noise-free measures are elusive for both, though for this discussion it is sufficient to illustrate only the one, testes weight. For a fuller discussion see Harcourt et al. (1981) and Dixon (2009). Some of the commonest sources of noise are as follows.

Some primate testes have been measured by weighing. In some cases, this occurs on removal while fresh but in others much later after being preserved. Sometimes the weight of the epididymis and other accessory tissue is included and sometimes not. Most testes, however, are measured in terms of dimensions while in situ using calipers. These dimensions then need converting into first a volume, then a weight. Thickness of the scrotal skin and differences in the size of left and right testes are sometimes accommodated and sometimes not. Some published reports are not even clear about whether the measures refer to one testis or two (e.g., the measurement of 27.10 g for *Papio hamadryas* in Harcourt et al. (1981, 1995) is almost certainly, to judge from the measures for single testes in Jolly and Phillips-Conroy (2003), for just a single testis, not the pair). Testis size is notoriously variable (e.g., Baker & Bellis, 1995; Dahl, Gould, & Nadler, 1993) yet sample size is often small (e.g., for *Colobus guereza*, $n = 1$ Dixon, 1987). No samples are collected using proper sampling protocol and usually no attempt has been made to correct for sampling bias. Noise due to season and age (Hamada, Suzuki, Ohkura, & Hayakawa, 2005) is also usually neglected.

Despite all these known sources of error, relative testes size is widely accepted as a proxy measure for the level of sperm competition (e.g., Anderson & Dixon, 2002; Dorus et al., 2004; Orr & Brennan, 2016). Moreover, the measure correlates not only with other suspected correlates of sperm competition across a wide range of animals (Simmons & Fitzpatrick, 2012) but also, for primates, with the direct measure of sperm competition level that we introduced previously for the Hominoidea (Baker & Shackelford, 2018). It would seem, therefore, that despite the noise in the data, the relative testes size signal (i.e., between-species variation) is strong enough to show through significantly in analyses.

4.2 | Signal-to-noise ratio: Sperm competition level calculated from paternity data

We accept that noise is generated at each step from the field collection of paternity data to the derivation of a figure for the sperm competition

level of a species. All potential sources of noise were appraised previously (Baker & Shackelford, 2018), and none was considered major. This new study of the Cercopithecoidea, however, has raised several issues that merit discussion.

4.2.1 | Noise generated by females not always containing sperm from the designated male in the ampulla at conception

The formulae developed in Baker and Shackelford (2018) are constructed to calculate the level of sperm competition experienced by Designated Males. If these Designated Males are chosen carefully, the mother of every young conceived in a study contains Designated Male sperm in her ampulla at conception. The sperm competition level experienced by Designated Males is then also the level for the sample. However, if the proportion of sampled females containing Designated Male sperm at conception falls below 100% then the formulae risk producing an overestimate of the sperm competition experienced by the Designated Male. This risk can be countered by adjusting the value of the variable POM (see Baker & Shackelford, 2018).

In almost all the field studies listed in Table 3, the females sampled can be confidently assumed to have sperm from their Designated Male in the ampulla at conception. This is particularly so when the Designated Male is either the only male in a uni-male group (S, Table 3) or a fertile-phase consort (C, Table 3). It is also highly likely when the Designated Male is a named individual because the probability of having sperm inside sampled females was the prime criterion used in choosing that individual as a Designated Male.

The situation in which the risk of females not containing Designated-Male sperm at conception would seem to be greatest is when the Designated Male is shown as the group's alpha in Table 3. This is particularly so when there are many rival males in the group and the group's multiple females have synchronous fertile phases (Altmann, 1962; Ostner, Nunn, & Schülke, 2008). The alpha male cannot guard all fertile females against all rival males continuously and may therefore, on occasion, fail to inseminate a given female during her fertile phase. How often this happens, however, is far from clear, largely because (§3.4) it is impossible for field observers to observe every mating a female performs during her usually 120 hr or so fertile phase.

Continuous observation is difficult enough by day and impossible by night (e.g., *Mandrillus sphinx*; Setchell, Charpentier, & Wickings, 2005) and matings with the eventual sire are often missed (see Dixon, Bossi, & Wickings, 1993). Some field observers even report that despite intensive observations and many recorded matings they did not see their target females mate even once with the male that eventually proved to be the sire, including when this sire was the alpha (e.g., *Macaca fuscata*; Soltis, Thomsen, & Takenaka, 2001). Failure to observe a given female mating with her Designated Male during her conceptive fertile phase is not evidence that she did not do so. To date, we know of no unequivocal evidence for any wild or free-ranging cercopithecoidea that a female ever conceives without containing sperm from a Designated Male (whether S, C, a, or named; Table 3). For the

purposes of this article, any noise from this possibility would seem to be minimal.

4.2.2 | Noise generated by errors in the assigned proportion of Other-Male copulations that are multiple-matings

Whenever there is ~100% probability that the Designated Male has sperm in a female's ampulla at conception it follows that any conceptive fertile phase mating by an Other Male is inevitably a Multiple Mating. Under such circumstances the parameter POM (percentage of Other-Male matings that are Multiple-Matings) is 100%.

So far in our studies of the Hominoidea and Cercopithecoidea only for humans is there evidence that the Designated Male (in humans, the female's long-term partner) does not always have sperm inside the female's ampulla at conception (see Baker & Shackelford, 2018). After lengthy analysis and discussion we calculated a value for POM of 95% in human societies that do not use contraception and 68% in societies that frequently use contraception. Further data would help to refine these assessments. As yet, however, as described above, we have found no unequivocal evidence for POM to be less than 100% for any non-human species of catarrhine, either hominoid or cercopithecoid. In this study, therefore, we have treated POM as a constant (=100%), not a variable, and conclude that any noise generated by the decision is likely to be minimal.

4.2.3 | Noise generated by errors in the calculation of fertilization bias

Although there are many and varied factors involved in Fertilization Bias (see Baker & Shackelford, 2018), we can here, for simplicity of discussion, reduce these to the number of fertile sperm present in a female's ampulla at conception. This then allows Fertilization Bias to become simply the number of fertile sperm present from the Designated Male divided by the number of fertile sperm present from the average Other Male. Any noise in the estimation of Fertilization Bias then derives from two main sources: the accuracy and appropriateness of the original authors' field data, analysis, and conclusions; and the accuracy with which the relatively simple procedure we use in Table 5 converts those conclusions by other authors into appropriate values.

Such noise can manifest itself in two ways. First, it can cloud existing differences in Fertilization Bias between species. Table 5, for example, concludes that the strongest Fertilization Bias in favor of the Designated Male is found in *Macaca fascicularis* and the weakest (in fact a bias in favor of the average Other Male) in *M. mulatta* and *M. sylvanus*. If these differences between species are misrepresentative then the signal-to-noise ratio in the complete set of calculated sperm competition levels will be reduced. Second, if the values of Fertilization Bias are inaccurate, they will reduce the accuracy of the calculated sperm competition level for each given species.

Although we cannot yet assess the level of noise generated by errors in our calculation of Fertilization Bias directly, we can assess

them indirectly from the performance of the final estimates of sperm competition level shown in Tables 6 and 7 that use them. On this basis, anticipating the outcome of the discussions below in §4.2.4 and §4.4, we conclude that whatever the level of noise generated by the estimation of Fertilization Bias in the different species it is insufficient to destroy either the overall signal or the accuracy of the estimate for the individual species.

4.2.4 | Signal-to-noise ratio

Whatever the total level of noise generated by the procedures and formulae used here to calculate sperm competition level, the evidence presented in §3 suggests that the signal remains strong enough to power an analytical tool. The primary evidence is that calculated levels of sperm competition correlate with levels of relative testes size. This is true for both the Cercopithecoidea (Table 7) and previously for the Hominoidea (Baker & Shackelford, 2018). Such strong or very strong correlations could not occur unless the signal-to-noise ratio for both measures is not only strong enough but also similar enough for such correlations to emerge. The two measures cross-validate each other, at least as independent proxies for sperm competition. Secondly, the comparison of calculated and theoretical data (Figure 1b) and of calculated and field data (§4.4) also add support to this conclusion.

4.3 | Comparison of paternity data and relative testes size as measures of level of sperm competition

Until relatively recently, paternity data were scarce and primatologists had little choice but to use relative testes size as a proxy measure for level of sperm competition. Now, though, that situation has changed. Although paternity data may not yet be more available than measures of relative testes size, they are at least equally accessible. Availability is no longer a factor.

If the use of relative testes size has any advantage as a measure of level of sperm competition, it is that testes size has evolved over the same or similar period as any other sexual characteristic that may invite assessment as an evolutionary product of sperm competition. Paternity data, on the other hand, can generate only the level of sperm competition at the time and place at which the data are collected. Therefore, if level of sperm competition has changed markedly in the recent past as has been suggested, in the Hominoidea, for gorillas (Stoinski et al., 2009) and humans (Dupanloup et al., 2003; van der Horst & Maree, 2014), then paternity data may not illuminate the evolutionary past as well as might relative testes size.

The data presented here and in Baker and Shackelford (2018) suggest that this potential advantage of relative testes size may not be as great in practice as it appears in principle, at least not for the Cercopithecoidea and Hominoidea. If there were a major mismatch in the information embedded within relative testes size and paternity data, the correlations between the two (Cercopithecoidea: Table 7. Hominoidea: Baker & Shackelford, 2018) would not be significant, or at least not as strongly as they are.

Against this uncertain but potential advantage of relative testes size, the advantages of the more direct measure of level of sperm competition yielded by paternity data are much more apparent. As detailed in Baker and Shackelford (2018) the two main advantages of the measures from paternity data are that (1) they are explicit and meaningful (e.g., males/conception) compared with the fairly inscrutable measures for relative testes size (e.g., % of body weight or residuals after log transformation; Table 2) and (2) varying as they do (see study-group values for OMP, Table 4) they can potentially be used to identify differences in sperm competition level between subpopulations and even socio-sexual groups in situations in which relative testes size varies little or not at all.

4.4 | Accuracy of calculated sperm competition level

Relative testes size is a proxy measure of sperm competition level, the values reflecting the relative sperm competition levels for a range of species but otherwise, as noted in §4.3, having little meaning. A value of 0.06 (%) or 0.0 (residual) could, for example, reflect a low, medium, or even high level of sperm competition.

At a minimum, the values generated from paternity data by the procedures used here could be viewed as similarly proxy measures. We have claimed (Baker & Shackelford, 2018), however, that when our procedure generates a figure of, say, 2.1, it means that at conception the sperm from a mean of 2.1 males are present in the female's ampulla at the moment of conception. The Cercopithecoidea have allowed a first opportunity to judge the accuracy of these figures.

As shown in §3.4, three field studies of female mating behavior during the conceptive fertile phase yielded observed numbers of males mating with a female during her conceptive fertile phase that were between 25% and 32% lower than our estimates of males/conception from paternity data. On average, this difference was roughly equivalent to the field workers missing females mating with a single male individual (range 0.49–1.33 missed males) per conceptive fertile phase. The absence of eventual sires from the list of observed mating partners (e.g., *Mandrillus sphinx*, Dixson et al., 1993; *Macaca fascicularis*, Engelhardt et al., 2006; *Macaca fuscata*, Soltis et al., 2001) verifies that this level of error frequently occurs in the field. On this basis, therefore, while acknowledging that the field data are limited, we contend that our calculated values are currently consistent with the mating events seen (and missed) in the field.

Further studies on a range of primates and other non-litter producing animals are necessary to evaluate the accuracy of our procedure further. However, on current evidence, we suggest that our method has the potential to become a powerful tool in future studies of the role of sperm competition in the evolution of sexual traits. Not least, it would allow a first empirical analysis of the role of sperm competition in the evolution of relative testes size that could then be compared with the wealth of theoretical analyses that already exist (Parker 2016). It could also be used to provide further analysis for such traits as sperm mid-piece volume (Anderson & Dixson, 2002) and seminal protein change (Dorus et al., 2004) for which suitable data already exist and for which conclusions so far have been based solely on proxy measures.

The hypothesis that this investigation was designed to test for the Cercopithecoidea was that paternity data, when processed as described, can provide a measure of sperm competition that is at least as useful as relative testes size. Insofar as the two measures showed a strong to very strong correlation, this hypothesis would seem to have been supported. Equally the similarities and differences between the calculated levels of sperm competition and the best figures that have so far been obtained from direct field observation of mating behavior were also reassuring given the known problems that exist with such field observations. We tentatively suggest, therefore, that when paternity data are available they offer a more practical or exploitable measure than relative testes size for future studies of the evolution of sexual traits.

CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

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